Biological Sciences: Ecology

Naturalization of European plants on other continents: the role of donor habitats

Short title: Naturalization of European plants

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Abstract

The success of European plant species as aliens worldwide is thought to reflect their ~~long-lasting~~ association with human-disturbed environments. However, an explicit test including all human-made, semi-natural and natural habitat types of Europe, and their contributions as donor habitats of naturalized species to the rest of the globe, has been missing. Here we combine two new databases, the European Vegetation Checklist and the Global Naturalized Alien Flora, to assess how human influence in European habitats affects the probability of naturalization of their plant species on other continents. A total of 9,875 native European vascular plant species were assigned to 39 European habitat types; of these 2,550 species have become naturalized somewhere in the world. Species that occur in both human-made habitats and semi-natural or natural habitats in Europe have the highest probability of naturalization (64.7% and 64.5% of them have naturalized). Species associated only with human-made or semi-natural habitats still have a significantly higher probability of becoming naturalized (41.7% and 28.6%, respectively) than species confined to natural habitats (19.4%). Species associated with arable land and human settlements were recorded as naturalized in the largest number of regions worldwide. Our findings highlight that plant species' association with native-range habitats disturbed by human activities, combined with broad habitat range, play an important role in shaping global patterns of plant invasions.

Significance statement

Understanding which species become successful aliens outside their native range is a fundamental question in ecology, as it informs efforts to mitigate ecological and economic losses from biological invasions. For alien plants of European origin, the association with human-disturbed environments is suggested as a key factor for their establishment success following introduction to other regions, especially to similarly disturbed human-made habitats. By combining a comprehensive list of European habitats and their species composition with a database of plant naturalization records worldwide, we showed that a broad habitat range together with human-induced disturbance experienced in native-range habitats can increase a species' chance of becoming naturalized in other parts of the world.

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Introduction

The role of species-habitat association as a factor driving patterns of plant invasions has become a key question in invasion ecology research (1). Comparisons of levels of invasion across multiple different habitats have shown that habitats differ in the number and abundance of alien species (2-5), but analogous habitats in geographically distant regions are invaded to a similar degree (6). Therefore, the most and the least invaded habitats within different regions remain essentially the same (6, 7). The observed patterns suggest that general properties of habitats in the invaded range, such as resource fluctuations and disturbance (8, 9), similarly affect levels of invasion in different parts of the world. In addition, evolutionary adaptations acquired in habitats in the native range are also likely to be important for invasion success (10, 11). Compared to those in the invaded range, the native-range habitats (i.e. the donor habitats of potential aliens) have been much less studied in the context of plant invasions (12, 13). However, recent studies indicate that native-range habitats differ in the number of invasive species they donate to other regions (14, 15), and the size of habitat-specific species pools in the native range affects the levels of invasion in corresponding habitats in the invaded range (16).

Once introduced to a new region, an alien species has to overcome several filters to survive in the local recipient habitats (17, 18). To match ecologically, the species has to possess traits that enable it to tolerate the range of local environmental conditions present. Since these traits evolved in the native-range habitats, conditions in these habitats act as an important factor affecting the invasion success of a species (11, 19-21). Previous studies comparing European natural and semi-natural habitats as donors of alien plant species to other parts of the world (15, 16) showed that species with the highest potential for naturalization (*sensu* 22) originated from habitats characterized by frequent and severe disturbances and high or fluctuating resource availability. Such conditions also promote the invasibility of habitats in invaded ranges (23). Species from such habitats often have higher probabilities to become successful aliens (10, 24) and are likely to constitute a large component of alien species pools (16). Invasion by alien species often begins in human-disturbed environments, where their propagules are unintentionally introduced or where cultivated species frequently escape (25, 26). Indeed, many early records of alien species come from human-made habitats (27), and these habitats tend to be more invaded than others (6, 28). While this is a well-known phenomenon, the role of human-made habitats as donors of alien plants has not been quantitatively assessed for the whole of Europe, with regard to other habitat types.

To test whether European habitats influenced by human-induced disturbances are the major donors of naturalized alien plants worldwide, we combined two recently compiled extensive datasets of unprecedented comprehensiveness: (I) the standardized classification of European vegetation (EuroVegChecklist; 29), which contains the most complete lists available of species associated with different vegetation types in Europe, and (II) the Global Naturalized Alien Flora (GloNAF) database, the most complete global inventory of naturalized floras (30). We focused on Europe as the source continent because it has donated disproportionally more species to the global naturalized alien flora than expected from the size of its native flora (30). To relate the naturalization probability of European native species to their association with particular habitats in Europe, we grouped European vegetation classes defined in EuroVegChecklist into 39 habitat types, defined on the basis of their vegetation. In parallel, vegetation classes were assigned to five naturalness categories: human-made (strongly human-influenced, n=9 classes assigned), semi-natural (moderately human-influenced, n=10), natural (not conditioned by human influence, n=71), human-made/natural (n=6) and semi-natural/natural (n=11). To quantify the naturalization frequency of European native species, we counted the number of regions where each species was recorded as naturalized in GloNAF, also including regions outside their native ranges that were located in other parts of Europe.

Specifically we asked which European habitats and naturalness categories (i) provide the highest number of species that naturalized outside their native ranges and (ii) donate species that have become established in the highest numbers of world's regions outside their native ranges.

Results

Habitat naturalness categories affect species' naturalization probability

Among the 9,875 species in our data set, the ones associated with European habitats classified to the human-made and semi-natural categories had a significantly higher probability to naturalize outside their native range, compared to natural habitat category (see GLM model; Table 1). Among species occurring only in habitats of one naturalness category, those from the human-made category were most likely to naturalize somewhere (41.7% of species in the cumulative species list of human-made habitats), followed by those from the semi-natural category (28.6%), while species from the natural habitat category were least likely to naturalize (19.4%). Moreover, species occurring in both human-made and natural or human-made/natural habitat categories, or in both human-made and semi-natural habitat categories (i.e.species with a broader habitat range), were even more likely to naturalize than those confined to the human-made category only. Of the species found in both human-made and semi-natural or natural habitat categories, 64.7% and 64.5% have naturalized (Table 2).

European habitats as donors of naturalized species

When comparing particular habitats, the highest numbers of naturalized species came from anthropogenic herbaceous vegetation, and temperate dry and mesic grasslands (Fig. 1a). However, when the size of the total species pool of a habitat was accounted for, human-made habitats, including arable land and alien-dominated forests, had the highest proportion of species naturalized in other regions. These habitats were followed by perennial ruderal vegetation, a habitat containing both human-made and natural vegetation types, and anthropogenic herbaceous vegetation (Fig.1b). Among semi-natural and semi-natural/natural habitats, mesic grasslands and pastures, and dry sand and rock-outcrop grasslands showed the highest proportions of species naturalized in other regions (Fig. 1b). The few natural habitats that had high proportions of naturalized species included riparian forests and riverine scrub, and hemiboreal mixed and temperate mesic deciduous forests. Of non-forest natural habitats, freshwater marshes, sea-grass beds and coastal sand vegetation had the highest proportions. In contrast, natural habitats with the lowest proportions of species that have naturalized were semi-deserts, various types of coniferous and evergreen forests and scrub, arcto-alpine grasslands, bogs and mires (Fig. 1b).

Naturalization frequency of European species

The naturalization frequency of European species outside of their native range was significantly higher for those species associated with habitats of the human-made category (Table 3); on average, they were recorded in the highest number of regions outside their native range compared to other habitat categories (Table 2). In contrast, the association of European species with habitats of the natural category significantly decreased their naturalization frequency (Table 3). Other habitat categories or their combinations showed no significant effect.

Detailed comparison of particular habitats showed that species associated with anthropogenic herbaceous vegetation had the highest naturalization frequency; collectively, they were recorded as naturalized in 83.8% of the GloNAF regions (Fig. 2). The second most represented were species from the human-made habitat arable land that were collectively recorded as naturalized in 73.6% of the regions, followed by species of various types of semi-natural grasslands collectively recorded as naturalized in 60.4% of the regions. Species of human-made/natural perennial ruderal vegetation have also naturalized in many regions (45.6% of the regions). Species of riparian forests and riverine scrub had the highest collective naturalization frequency among natural habitats (55.6% of the regions). In contrast, species from stressful natural habitats with nutrient-poor soils and extremely low or high moisture conditions (29), such as bogs, waterlogged and dry forests and scrub (Fig. 2), have naturalized in the lowest numbers of regions.

Species capable of naturalization in the largest numbers of regions originated mainly from European anthropogenic herbaceous vegetation, arable land or from both these habitats and semi-natural or natural grasslands. A list of species and their donor European habitats with the highest numbers of regions where they have naturalized is shown in SI Appendix, Table S3.

Discussion

Our study provides clear evidence that European species occurring in both human-made and other habitat categories are more likely to naturalize in new regions compared to species confined to either human-made or semi-natural habitat categories alone. However, species of strongly human-influenced habitats in the human-made category or moderately human-disturbed habitats in the semi-natural category are also highly likely to naturalize outside their native range. Because Europe is one of the main donors of alien plant species to other parts of the world (19, 30, 31), the association of European species with human activities in their native range may be a major determinant of their success as aliens on other continents (19, 32-34). Our study is among the first to empirically support this long-standing but so far untested hypothesis.

Species of human-made and semi-natural habitats are most likely to naturalize

The association of species with human-made and semi-natural habitats in their native range favors naturalization elsewhere, as indicated by our results. Species associated with these habitats are more likely to naturalize than those confined to natural habitats in their native range. Species of the former habitat categories thus appear to be pre-adapted to establish populations at human-disturbed sites created by human agency around the globe. One possible explanation is that the long-term association of species with human-disturbed environments in Europe led to evolution of suitable traits that facilitate establishment in similarly human-influenced habitats of the invaded range (19, 34).

An alternative explanation could be that human-induced disturbance sets strong filters for species arriving in human-made habitats of Europe from the regional species pool and thus only those with suitable traits can establish (35, 36). The latter mechanism does not require the evolution of necessary traits in human-made habitats; instead it assumes selection of pre-adapted species with such traits from the regional flora in the native range.

Many species of European anthropogenic or weed vegetation are, within Grime's CSR life-strategy framework (37), R-strategists that can withstand frequent disturbances by having persistent seed banks and fast regeneration. They are likely to require recipient habitats with regular disturbances which decrease competition with established native plants. Human-made and natural perennial ruderal vegetation in Europe mainly consists of herbs with C- or CRstrategies with vegetative reproduction that enables survival under moderate levels of disturbance (38, 39), but these species are also successful competitors in natural habitats. Many of them are effectively dispersed by humans or wind, which supports their spread outside their native ranges (38, 40). Species of human-made habitats are also associated with naturally nutrient-rich or anthropogenically nutrient-enriched sites (41). The ability to utilize high resource levels for fast growth is considered typical of successful alien species (18, 42).

The greater naturalization frequency of European species associated with human-made habitats may further be attributed to the fact that species frequently occurring in densely human-populated areas in their native range are more likely to be introduced to new regions (12, 42). This applies to species restricted to human-made habitats and the ones that also occur in more natural habitats, but the latter are more likely to be dispersed by humans because they tend to be more widespread in their native range (43). Also, species restricted to human-made habitats that often occur in the vicinity of transportation systems or that are directly utilized by humans have a high chance of human-assisted long-distance dispersal (44, 45). It is likely that the observed pattern of donor habitats results from a combination of species traits gained or filtered in strongly or moderately human-influenced habitats, and a higher introduction rate leading to greater propagule pressure. However, understanding their relative contributions requires further research.

Many species of various types of European semi-natural mesic and dry grasslands were identified as naturalized in many regions worldwide. These European grasslands have been used by humans for a long time (46, 47), and their species pools are thus adapted to human disturbances, which may facilitate the initial phase of spread in strongly or moderately human-influenced habitats in new regions. While some species of dry grasslands were introduced as contaminants of seeds and crops (45), others were introduced intentionally to improve pastures (46, 47), and were grown at high population densities on grazing land, which could unintentionally have increased the propagule pressure and facilitated escape from cultivation and subsequent naturalization (48). However, higher naturalization frequency is not associated with the semi-natural category as a whole. Other semi-natural habitats such as mires, fens and springs or heathlands that are confined to sparsely populated, high-elevation areas decrease the chance that species are picked up and transported, thus reducing the contribution of naturalized species from this habitat category.

Species confined to natural habitats in their native range are less likely to naturalize

Compared to human-made and semi-natural habitats, natural habitats are generally moderate to poor donors of naturalized species. However, many naturalized alien species were also donated by habitats that frequently experience natural disturbance, by nutrient-rich and highly productive riparian forests and riverine scrub, and eutrophic forests. This indicates the importance of alien species adaptation to conditions induced by natural disturbance processes that are similar to those in human-made habitats in new regions. Indeed, disturbances and nutrient enrichment - factors selecting for species that are able to successfully establish in new regions - together with increased probability of species transport have been previously suggested as causes of high numbers of alien species coming from European riparian forests (14-16). Coastal habitats including sea-grass beds and coastal dunes have also been shown to be important donors of alien species that can profit from adaptation to frequent natural disturbances in dynamic environments (15). Moreover, these habitats are usually found in lowlands and close to coastal regions that are more densely populated, where increased opportunities for effective species transport can play a role (15, 16).

In contrast, poor donors of naturalized alien species include natural habitats with nutrient-poor soils and stressful site conditions at both ends of the moisture gradient, such as bogs and bog woodlands, mires, saline vegetation, heathlands, xeric scrub and semi-deserts.

This is also in accordance with previous findings that only few invaders are adapted to stressful conditions (49). Some of these habitats are small and isolated, often at high elevations, while others cover vast areas. Nevertheless, in all of them the human influence is negligible because of low human population densities in these areas. Therefore, it is difficult to distinguish between the effect of adaptation to stressful conditions that prevent establishment in human-disturbed productive habitats (8, 49), and a lower probability of species introduction to new regions.

Species occurring in multiple habitat categories are more likely to naturalize

We show that European species associated with both human-made habitats and natural or semi-natural habitats in their native range are more likely to naturalize outside their native range, than species associated exclusively with human-made or semi-natural habitats. According to the concept of anthropogenically induced adaptation to invade (50), two types of adaptation to human disturbances can evolve in the native range. First, habitat generalists adapted to both natural and human-influenced habitats in the native range, i.e. having broad habitat ranges, can naturalize more easily in the new region regardless of how the invaded habitats are influenced by humans. Second, habitat specialists that are adapted to strongly human-influenced habitats (50) are less likely to invade habitats that are little affected by human activities. Our results indicate that high invasion success is to be expected for those generalist species (12, 51) with multiple native-range habitats including those that are human-made. Indeed, the importance of a broad native habitat range has been reported for naturalization of Central-European plants in North America (52). Species that have a broad habitat range are likely to tolerate a broad range of conditions, both biotic and abiotic, and may develop better competitive abilities through interactions with various species (53). Thus, naturalized species have probably benefited from broad habitat range as well as the association with human-made or semi-natural habitats, making them preadapted for establishment in human-influenced habitats outside their native ranges.

Other factors influencing naturalization probability

The pattern of habitats in Europe acting as donors of naturalized alien plants globally could result from life form instead of disturbance and introduction probability. Indeed, six out of eight habitats with the highest proportions of species naturalized in other regions are herb-dominated, and habitat types are defined here partly through dominant life forms. However, the effects of life form can be context-dependent. For example, an asymmetry has been found for Europe, which donates many more naturalized species from its herb-dominated grasslands than it receives from similar habitats on other continents (10). In our study, only the direction of introduction from Europe is considered, hence the role of herbaceous life form on the probability of naturalization needs to be considered with caution. If other inter-continental directions were to be assessed, the most common naturalized species might not be herbs (54).

Other factors such as residence time and geographic origin of species may also be important for species' success as aliens (14). However, our analysis included species of the same invasion status, i.e. naturalized neophytes, and of the same geographic origin, and so these confounding factors should be significantly reduced. Although habitats are complex units defined by many underlying factors, those that are the most important donors of naturalized species share one property, which is frequent disturbance, often human-induced.

Species of European human-made habitats are able to naturalize in many regions

~~Invasions by generalist species contribute to the taxonomic, functional, and phylogenetic homogenization of biotas (49, 50).~~ Our results clearly show that alien species associated with human-made habitats in Europe invaded the majority of regions included in the GloNAF database (up to 84% of the regions for species of anthropogenic herbaceous vegetation). The strong human alteration of environmental conditions renders human-made habitats similar in many respects across the world, despite their different biogeographical locations (55, 56). High levels of invasion in human-made habitats (6) can be caused by larger alien species pools or by a higher chance for species to be transported to new regions (51). More incoming species results in higher colonization pressure in such habitats (57), and species that successfully establish increase their abundance and produce more propagules, facilitating their further spread (58).

Human-made and natural perennial ruderal vegetation donated the most naturalized species on average compared to other habitats, but these species were not recorded in the largest number of regions. This suggests that species occurring in both human-made and natural habitats are somewhat limited in their ability to establish in multiple regions. Their occurrence might reflect suitable climate, because different natural habitats occur in contrasting climatic regions of Europe and thus their species can have stronger requirements for a climatic match between native and non-native regions than species confined to human-made habitats only.

We predicted that the specific nature of human-made habitats contributes to a wider geographic range of alien species adapted to them. Indeed, we found that species of human-made habitats are naturalized in many regions worldwide. However, it is important to note that the number of regions is only an approximation of the invaded range size, because GloNAF regions differ in their sizes, and it remains unclear to what extent particular regions have been colonized. Also, we have no information on the representation of different habitats in invaded regions. If the origin of species in strongly human-influenced habitats facilitates their establishment in similarly disturbed habitats elsewhere, then a higher abundance of those habitats in the invaded region can increase the probability that species are recorded there. Nonetheless, the number of regions in which a species was recorded as naturalized is the best proxy of naturalization frequency available at a global scale, and strongly correlates with the cumulative area of these regions (59).

Conclusions

Our study represents, so far, the most comprehensive analysis of the role of native-range habitats on worldwide naturalization probability and extent of alien plants of European origin. European species that occur in human-made and other habitats at the same time, or in human-made and semi-natural habitats alone, have higher probabilities to naturalize outside Europe than species confined to natural habitats only. Therefore, broad habitat range and association with disturbed, human-influenced habitats in the native range belong among important factors contributing to species' naturalization success. Further work is needed to gain a more detailed insight into the effect of donor habitats on the various invasion outcomes of species at the global scale.

Materials and methods

Data on European habitats and their species composition

Our data set included habitat types and their associated plant species, derived from the new hierarchical classification system of European vegetation (EuroVegChecklist; 29). A version of the EuroVegChecklist species list from October 2014 was used for this study. Bryophytes, lichens and algae were excluded from the list, and the scientific names of the remaining vascular plant taxa were standardized according to The Plant List (http://www.theplantlist.org) using the package Taxonstand v 1.0 (60) in R (61). Infraspecific taxa, i.e. subspecies and varieties, were merged at the species level. Species with currently unresolved taxonomy in The Plant List as well as 550 species not native to Europe were excluded. The final list comprised 9,875 vascular plant species, a significant proportion of the total European native flora (c. 12,500 species; 62).

From 109 phytosociological classes of European vegetation recognized in EuroVegChecklist (29), two classes, one endemic to Greenland and one to Cyprus, were excluded. All other classes covering vegetation types of continental parts of Europe, Arctic archipelagos and Macaronesian islands were subjected to two merging procedures. Firstly, classes were grouped into habitat types considering the similarities in vegetation physiognomy, dominant life form, species composition, ecology and biogeography as described in EuroVegChecklist, the EUNIS Habitat Classification (63), the European Red List of Habitats (64) and the Map of Natural Vegetation of Europe (65). In total, 39 habitat types (also called habitats in this paper; SI Appendix, Table S1) were defined. On average, 145±192 (mean±SD) vascular plant species were assigned to each habitat from the final list. Secondly, habitats were further grouped into five habitat categories according to the degree of naturalness (see SI Appendix, Table S1) based on the descriptions in EuroVegChecklist (29). Each category contained an average 2,442±2,004 species (SI Appendix, Table S2). The categories included: (i) human-made habitats, (ii) semi-natural, i.e. moderately human-influenced habitats and (iii) natural, i.e. those habitats whose existence is not conditional on considerable human intervention. However, because some phytosociological classes can develop both in natural and human-influenced sites, we subjectively defined two other categories: (iv) human-made/natural habitats and (v) semi-natural/natural habitats. The human-made/natural habitat category includes perennial ruderal vegetation that occurs both at strongly human-influenced sites in and around human settlements and at naturally disturbed nutrient-rich sites such as floodplain forest fringes, river banks and windthrow sites. It also includes a group of plant communities occurring both on inland cliffs and walls. The semi-natural/natural habitat category includes various types of grasslands and scrub that can develop both naturally and as a result of moderate human intervention at potential forest sites (29).

Data on worldwide naturalization of European species

For each of the 9,875 vascular species native to Europe in our final species list of European habitats, the status as naturalized aliens somewhere in the world, irrespective of whether it was inside or outside of Europe, was identified using the GloNAF database (version 1.1; 30, 59). Naturalized aliens included those species that create self-sustaining populations in a given region without human intervention and recruit freely, but do not necessarily spread over large areas (22). This database includes national and sub-national inventories of naturalized alien plant species in 843 regions worldwide. The list of standardized scientific names of species in European habitats was matched to the GloNAF database, revealing 2,250 species to be naturalized outside their native range. Of these, 474 species were reported as naturalized only within Europe (i.e. in regions within this continent other than where the species is native to; see 28), 715 as naturalized only outside Europe and 1,061 as naturalized in both. Only naturalized species known as neophytes were considered, i.e. those introduced outside their native range after 1500 AD (59). Archaeophytes (species introduced before 1500 AD) were not considered because their classification varies among European regions (66) and is not available for other regions of the world (30).

Data analysis

To test whether species from the habitat naturalness categories differed in their probability of naturalization somewhere in the world (irrespective of the number of regions where they are naturalized), we applied a generalized linear model (GLM) with a Bernoulli distribution. Because some species occur in two habitat categories at the same time or in one or both of the two combined habitat categories (human-made/natural habitats or semi-natural/natural), we converted the habitat-category variable into three dummy variables, each with two levels (67): human-made, semi-natural and natural. Species from combined habitat categories were assigned to the two corresponding habitat categories. Species in the human-made/natural habitat category were assigned to both the human-made and the natural main categories and analysed together with species occurring in the human-made and natural category at the same time. Similarly, species in the semi-natural/natural habitat category were assigned to both the semi-natural and natural main categories and analyzed together with species occurring in the semi-natural and natural category at the same time. As main effects, we included three dummy variables: human-made (yes, no), semi-natural (yes, no), and natural (yes, no). To test whether the effect of a habitat type on naturalization of a species also depends on the species occurence in another habitat type, we also included all two-way interactions between the dummy variables (human-made:-natural, human-made:semi-natural, and semi-natural:natural). No combined habitat category human-made/semi-natural was distinguished among habitats, thus the interaction human-made:semi-natural includes only species occurring in both categories. We also tested the effect of species association with main habitat naturalness categories and their two-way interactions in Europe on the number of GloNAF regions worldwide in which species have naturalized, i.e. naturalization frequency. Numbers of regions were ln--transformed and species that were not naturalized in any region were excluded. To facilitate interpretation of the model estimates, each of the dummy variables was centred to its mean value (67). The analysis was performed using the glm function in R (version 3.1.2; 61). Total variation explained by the model was calculated following Nakagawa & Schielzeth (68).

At the scale of individual habitats, we calculated the proportion of species native to Europe that have become naturalized somewhere, relative to the number of all species assigned to the given habitat to account for the size of the habitat species pool. To compare the frequency of naturalization, we also calculated, for each habitat, the total number of regions where at least one representative of that habitat is reported as naturalized. Finally, we identified those species within the final list that have become naturalized in the highest numbers of regions. All 2,250 naturalized species identified were analysed together regardless of the regions where they were naturalized, i.e. outside Europe, within Europe or in both.

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Figure legends

Figure 1. A comparison of 39 European habitats as donors of native plant species that have naturalized in other regions. Numbers (a) and proportions (b) of those species per habitat are shown. Naturalness categories are indicated by different filling patterns (see text for classification criteria).

~~Figure 2. A comparison of species naturalization frequency, measured as the number of regions worldwide (n = 843, based on GloNAF) in which native Europan species associated with given naturalness habitat category in Europe have naturalized. Kruskal-Wallis test (Q = 216.5, P<0.001), group differences are indicated by letters (multiple comparison of mean ranks, P<0.05), median (line), 25–75% (box) and 5–95% quantiles (whiskers) are shown. N = number of species assigned to the naturalness category.~~

Figure 2. A comparison of naturalization frequency of plant species as the total number of world’s regions where any of the native species from the given European habitat are recorded as naturalized. Naturalness categories are indicated by different filling patterns.